THE GOODENIACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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GOODENIACEAE R. Brown, Prodr. Fl. Nov. Holland. 1: 573. 1810, "Goodenoviae," nom. cons.

(GOODENIA FAMILY)

A very natural family of shrubs and herbs with usually alternate, exstipulate leaves; complete, bisexual, proterandrous, 5-merous flowers; irregular corollas; 5 free stamens; commonly 2-locular, usually inferior ovary; and a style bearing at the apex a pollen-collecting cup ("indusium") which subtends the stigma. TYPE GENUS: *Goodenia* J. E. Sm.

Eight of the fourteen genera are restricted to Australia. Of the six which also occur outside of Australia, *Selliera* and *Scaevola* are especially remarkable for their distributions, the former subantarctic (Australia, Tasmania, New Zealand, and Chile), the latter pantropical. Goodeniaceae are notable for their almost exclusive confinement to rather arid or periodically dry regions with open vegetation.

The chief peculiarity of the flowers is a pollen-collecting cup, which has attracted the attention of numerous botanists. This structure, comparable to, although not homologous with, the ring of stylar hairs in some genera of Campanulaceae, is perhaps a more specialized type of the same biological nature. The anthers closely surround the cup, and the pollen, which is released when the flowers are still in bud, is deposited in the cup (FIG. 1b). At this stage the stigma is very small and nonreceptive (FIG. 1d, e). During anthesis the pollen is shaken out by insect visitors or is forced out of the collecting cup by the growing stigma. After the pollen is removed from the collecting cup the stigma becomes receptive

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39:** 296–346. 1958) and continued to the present paper. The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary information in brackets. References which the author has not seen are marked by an asterisk.

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(FIG. 1f, g). Although self-fertilization has been reported, cross-fertilization seems to be the rule. Floral anatomical evidence suggests that the two- to one-locular ovary of Goodeniaceae is derived from four carpels (Carolin).

Development of the embryo seems to follow the Linum variation of the Solanad type. The embryological features of the family (ovules with one integument and thin nucellus, primary archesporium usually unicellular, monosporic 8-nucleate embryo sac, cellular endosperm, absence of haustoria, and the type of embryo development) suggest a relationship with Campanulaceae. Chromosome numbers of $2n = 14$, 16, and 18 appear to be typical for the genera of Goodeniaceae, with polyploids with $2n = 32$, 36, 48, 54, 64, 72, and 90 occurring at the specific and infraspecific levels.

Despite an abundant literature concerning the anatomy of the family, further comparative studies may be of taxonomic interest. The occurrence of three- to five-lacunar nodes and the presence of inulin as a storage carbohydrate in Goodeniaceae are notable.

Goodeniaceae are generally accepted as closely allied to the Campanulaceae-Lobelioideae (but cf. Carolin, 1960b) from which they differ chiefly in the lack of latex, in the presence of a pollen-collecting cup, and in the more complex anatomy of the cambial tissue. The monotypic Australian family Brunoniaceae (*Brunonia australis* J. E. Sm., $2n = 18$) is the closest relative of Goodeniaceae and has often been united with them. A relationship with Stylidiaceae is also presumed.

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1. **Scaevola** Linnaeus, Mant. Pl. Alt. 145. 1771, nom. cons.[2]

Shrubs [or herbs] with alternate [rarely opposite], simple, entire [or toothed], fleshy, isolateral [or bifacial], exstipulate leaves. Inflorescences axillary, simple to few-flowered compound dichasia sometimes reduced to a single flower, the terminal (central) flower sessile [or pedicellate] in the fork. Floral tube adnate to the ovary; calyx limb short, inconspicuously [or conspicuously], usually unequally, 5-lobed to subentire. Corolla white [yellow, purplish, or blue], 5-lobed, the long tube open to the base on the adaxial side, densely woolly inside, the lobes provided with very thin, membranaceous wings which are sharply folded inward in bud (induplicate-valvate). Stamens 5, alternate with the petals, free, with a conspicuous, cushion-like nectar gland[3] between the 2 abaxial ("anterior") stamens and a minute gland next to the odd adaxial ("posterior") stamen; filaments slender, ± equaling the corolla tube; anthers introrse, basifixed, 2-locular at anthesis, provided at tip with a small ± ovate appendage (prolongation of connective), longitudinally dehiscent; pollen usually medium, subprolate, 3-colporate, punctulate to subreticulate, 2-nucleate. Gynoecium 4-carpellate, appearing 2-carpellate, syncarpous; stigma slightly 2-lobed, subtended by a ciliate pollen-collecting cup ("indusium") hairy [or glabrous] without; style elongated, ±cylindrical, simple, hairy at base; ovary inferior, 2-locular [or 1-locular]; ovules usually solitary in each locule, anatropous and epitropous, ascending from base of partition, 1-integumented, with a thin nucellus. Fruit a juicy [or nutlike], blue-black [or white], 1- or (more rarely) 2-seeded drupe; endocarp bony [or with a corky outer layer], irregularly warty to subreticulate on the surface. Seed whitish, obovate in outline, planoconvex in cross section; seed coat thin, soft; endosperm fleshy; embryo straight; cotyledons flat [or ± semicircular in cross section], inequilaterally elliptic, divergent; radicle short, inferior. TYPE SPECIES: *Lobelia Plumieri* L. = *S. Plumieri* (L.) Vahl (*S. Lobelia* Murr., nom. illegit.).[2] (Name from Latin, *Scaevola*, a diminutive of the Roman surname *Scaeva*, the Left-handed, apparently after a legendary one-handed Roman hero,

[2] Although the conservation of *Scaevola* L. is unnecessary (see Rickett & Stafleu, Taxon **9**: 122. 1960, and the International Code of Botanical Nomenclature 315. 1961), retention of this name in the list of *Nomina Generica Conservanda* of the Code was authorized by the International Botanical Congress in Montreal in 1959.

Conservation of the type of *Scaevola* also appears to be unnecessary. Having established the genus *Scaevola*, Linnaeus mentioned under *Lobelia* (Mant. Pl. Alt. 481. 1771) a single species, "Lobelia *plumieri*. *Scaevola* distincti generis," which, although not transferred by Linnaeus to *Scaevola*, became automatically the type of the genus. However, *L. Plumieri* L., of the *Species Plantarum* (as well as *Scaevola Lobelia* Murr., nom. illegit.), was a mixture of two species, the Indo-Pacific and Indo-Atlantic beach-berries. After Gaertner (Fruct. Sem. Pl. 1: 119. 1788) segregated the Indo-Pacific species as *Lobelia Taccada* from *L. Plumieri*, the Indo-Atlantic species retaining the specific epithet *Plumieri* became the type of *Scaevola*, as *S. Plumieri* (L.) Vahl.

[3] This character, observed in *Scaevola Plumieri* and *S. Taccada*, apparently has not been reported previously for the genus.

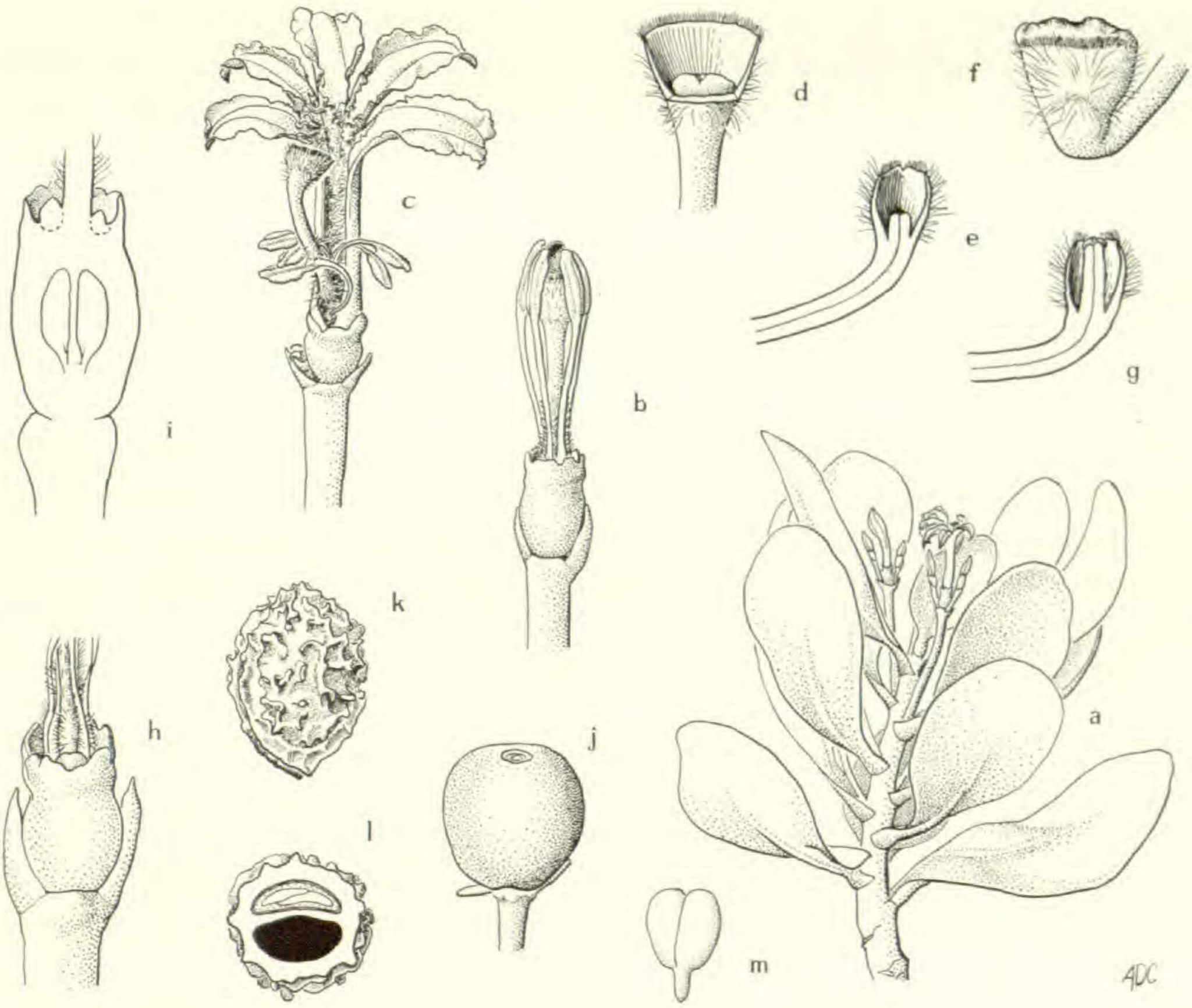

FIG. 1. **Scaevola.** a–m, *S. Plumieri*: a, flowering branch, × 1/2; b, flower bud, corolla removed to show pollen-collecting cup and introrse anthers at time of dehiscence, × 2; c, flower, from adaxial side, × 1 1/2; d, collecting cup at time of dehiscence of anthers, one side removed to show undeveloped stigma, × 4; e, cup, undeveloped stigma, and style (with stylar canal) at anthesis in semidiagrammatic vertical section (at right angles to "d"), × 4; f, mature stigma protruding from collecting cup, × 4; g, same, in semidiagrammatic vertical section, × 4; h, base of flower from abaxial side, corolla removed to show large nectar gland (protruding above calyx lobes), × 3; i, ovary in diagrammatic vertical section to show large abaxial nectar gland, small adaxial gland, and solitary epitropous ovules, × 4; j, mature fruit, × 1; k, stone, × 2; l, stone in semidiagrammatic cross section to show seed (endosperm stippled, cotyledons white) and empty locule (black), × 2; m, embryo, × 2.

Gaius Mucius Scaevola, because of the corolla somewhat resembles the shape of a man's hand.) — BEACH-BERRY.

The genus comprises about 80 species, 60 restricted to Australia. Most of the remaining species belong to the almost exclusively extra-Australian sect. SCAEVOLA (§ *Sarcocarpaea* G. Don), centered in the Pacific, but with two littoral species, *Scaevola Taccada* (Gaertn.) Roxb. (*S. frutescens* Krause, *S. sericea* Vahl), $2n = 16$, and *S. Plumieri*, $2n = 16$, of wide tropical distribution. The former species is confined to the Eastern Hemisphere, ranging from Madagascar and Mauritius to Ceylon and through southeastern Asia, Malesia, and tropical Australia to the central Pacific,

while the latter is distributed from Ceylon and India to Mauritius and Madagascar, and around tropical Africa to tropical America, the West Indies, southern Florida, and Bermuda. In southern Florida, *S. Plumieri* occurs from Key West northward to about Brevard County, on the east coast, and sporadically on the west coast, mostly on islands (with the exception of Pine Island, Lee County, and one or two others), to the mouth of Tampa Bay. Beyond our area the species has been recorded in the United States from Padre Island, Texas, and very sporadically on both coasts from southern Baja California and Yucatán to Ecuador and Brazil. A pioneer species on fresh calcareous sands of the upper beach and foredunes, *S. Plumieri* is usually associated with other dune-binding species, e.g., *Ipomoea stolonifera* (Cyrill.) J. F. Gmel. and/or *I. Pes-caprae* (L.) R. Br., *Uniola paniculata* L., *Croton punctatus* Jacq., *Tournefortia gnaphalodes* R. Br., and *Suriana maritima* L. It usually grows in dense clumps, sometimes forming large patches as it slowly spreads under the sand by stolons rooting at the nodes. The irregular distribution of *S. Plumieri* is probably due primarily to its rather low resistance to the destructive action of hurricanes and gales and locally to the action of cattle and goats which eat the entire plant.

Despite the existence of many inland species growing in rather diverse habitats, the genus seems, in general, to be adapted to a littoral life. The thick cuticle and epidermis, the massive development of palisade tissue, the development of water-storage parenchyma, and also, in some species, of water tracheids (*Scaevola Plumieri*, *S. crassifolia* Labill.) and/or mucilage cells (*S. Taccada*, *S. crassifolia*) in the leaves are regarded as xerophilous adaptations in littoral species. A resinous substance excreted by the peltate glandular hairs presumably protects young organs from desiccation. Stomata usually occur on both leaf surfaces. A number of primitive features (scalariform perforation plates, diffuse axial parenchyma, and a tendency toward transitional intervascular pitting) have been found in the wood of a few species of sect. SCAEVOLA (*S. Plumieri*, *S. Taccada*, and *S. Gaudichaudiana* Cham., $2n = 16$).

Large bees have been mentioned as very frequent visitors of the flowers of *Scaevola Taccada* and bees and butterflies of *S. Plumieri* (in South Africa and Madagascar). Chromosome numbers, known in about 30 species, are almost invariably $2n = 16$, but tetraploids and/or hexaploids ($2n = 32$ and 48) have also been found in three species.

The fleshy drupes of sect. SCAEVOLA are very probably dispersed locally by birds, but the stones of some species of this section (*Scaevola Plumieri*, *S. Taccada*, and *S. mollis* Hook. & Arn., $2n = 16$) and of sect. XEROCARPAEA G. Don (*S. porocarya* F. Muell., $2n = 16$, *S. crassifolia*, *S. globulifera* Labill., $2n = 16$, and *S. thesioides* Benth.) have been reported as water borne and liable to dispersal by sea currents. These stones usually owe their buoyancy to a corky outer layer (*S. Taccada*) sometimes in accompaniment with empty lacunae in the endocarp (*S. mollis*, *S. porocarya*). Stones of *S. Plumieri* lack a corky layer, but usually only one of the two locules holds a seed, and the empty locule is watertight,

giving floating power to the stone. It is noteworthy that of all the species with buoyant stones only *S. Taccada* and *S. Plumieri* are widely distributed. Guppy showed that stones of the former can float in sea water for a year or more, while those of the latter can, on the average, endure in a sound condition for only four or five months.

Scaevola is closely related to *Goodenia* and *Verreauxia* Benth. The genus is in need of a taxonomic revision.

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